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THE GEOLOGICAL AND GEOGRAPHICAL RELATIONS OF THE LAND-BIRD FAUNA OF NORTHEASTERN AMERICA.

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THE antiquity of existing faunas is a problem beset with difficulties and involved in obscurity. One who fares forth in this quest will find few landmarks to serve him as a guide. No evidence from fossil remains is forthcoming, for the deposits in which recent animals have been buried are as yet incoherent muds and silt, often beneath the waters of lakes and swamps and tidal inlets. The remains of mammals and reptiles may thus have been accumulating in many places over long periods of time, since the beginning, at least, of post-glacial conditions. Undoubtedly the soils of old forest floors and peat bogs and the mud of lake bottoms contain a vast number of such remains, but it is altogether unlikely that among these is any large proportion of the more fragile skeletons of birds. Even if they were preserved these remains, like those of other creatures, would still be in inaccessible situations. The clew to this history of faunas is to be looked for rather in the distribution of living forms as we find them to-day; to facts relating to the alteration of habitats, the invasion of new territory by certain species, the recession from territory once occupied, and the dominance and variety of forms of particular genera in various localities.

[1] Read before the Delaware Valley Ornithological Club, Philadelphia, March 4, 1909.

The present paper is the outcome of an article previously published by the writer in 'The Popular Science Monthly'[1] which dealt with the effect of the settlement of the country upon the distribution of bird life, what we might term the bird life under aboriginal conditions as compared with its present aspects. The problem as stated in that article was this: If eastern North America was in the main a forest-covered land, as both historical narrative and existing physical conditions indicate, what was the status of the bird life that now inhabits our open fields and grass country? Have certain birds altered their *habits* or their *habitats*? Facts seem to point to the last named of the two alternatives as offering the mostly likely solution to the problem since most of our grass-frequenting species are of wide distribution toward the west, throughout the prairie region, and many of them are represented by geographical races on the Great Plains. Such species as the Vesper Sparrow or Grass Finch, the Savannah and Grasshopper Sparrows, the Meadowlark, Bobolink, and Red-winged Blackbird, the Killdeer and Grass Plover were cited in illustration, and I stated my belief that these birds had found their way into the newly opened lands from the western prairie region. An exception might be made in certain species — that of the Bobolink which may have frequented the river marshes, and also in the case of the Savannah Sparrow which appears to be a coastwise bird, dwelling along the edge of the maritime marshes, though its present habitat may be a comparatively recent occupancy. The Black-throated Bunting or Dickcissel was cited as a remarkable case of recession from its one time habitat in certain eastern localities during the latter half of the nineteenth century, and there is good evidence for believing that this bird was originally an invader from the prairie region. Its great abundance in the grass country of the Middle West and its rather limited distribution in the East, coupled with its somewhat abrupt disappearance from the last named region, certainly point to this conclusion. Audubon speaks of its abundance in the prairie lands of Texas, Missouri and Illinois as compared with the middle Atlantic districts and that it was "rarer in Ohio, and scarce in Kentucky," which is good evidence, for at the

[1] 'Birds of the Grasslands.' The Popular Science Monthly, Vol. XLII. p. 453, February, 1893.

time of which he writes Ohio and Kentucky were still covered with much woodland. He further adds, "they are rarely observed to pass over South Carolina," a statement that would indicate that this species did not migrate along the coastal plain from the south, but spread eastward from its main prairie center of distribution.

So much for this aspect of the problem which is here briefly reviewed. There is abundant room for further research into the past and present relations of our eastern bird fauna, and it is the purpose of this paper to point out certain facts that seem to indicate changes in the status of the bird population of various districts. It is hazardous to attempt to draw conclusions as to the past history of a fauna from such slight evidence as the present distribution of species, but some irregularities in the distribution of certain species of birds seem to have been remotely the result of certain geological processes, at least within the post-glacial period. What evidence I have to offer in support of this statement is as follows: For a number of years I resided during the summer months (from mid-June to September) at Barrington, Nova Scotia. Barrington lies just back of Cape Sable Island at the extreme southern end of the peninsula. The general aspect of the surrounding region is that of a typical boreal country — a coniferous forest, composed mainly of spruces and balsam fir, interspersed with tamarack swamps, sphagnum moors with their associate flora, notably Labrador tea (*Ledum*), Rhodora, and several species of *Vaccinium*, thickets of the northern alder, and aspens and birches. The bird fauna is decidedly Canadian in its character, such forms as the Olive-backed and Hermit Thrushes, the Hudsonian Chickadee, the Golden-crowned Kinglet, the Red-bellied Nuthatch, the Nashville, Yellow Redpoll, Magnolia, and Myrtle Warblers, the Junco, the White-throated Sparrow, the Solitary Vireo, the Rusty Blackbird, the Canada Jay, the Alder and Olive sided Flycatchers, and the Black-billed Cuckoo being more or less abundant throughout the breeding season, while the Pine Grosbeak, the Pine Siskin, and both species of Crossbills were abundant during certain years in the breeding time, but conspicuously absent in other summers. With this assemblage of Canadian birds were many other widely spread species as the Robin, the Song Sparrow, the Black and White, Chestnut-sided, and Yellow Warblers, the Savannah

Sparrow, the Purple Finch, the Barn, Cliff, and Tree Swallows, the Nighthawk, Flicker, and others, but such wide-ranging forms as the Bluebird, the Vesper Sparrow, the Chipping Sparrow, the Goldfinch, and the Meadowlark were never observed during the six summers spent in this region, while the Kingbird only appeared at the latter end of the summer, about the last of August or early in September, though breeding in more or less abundance in districts farther to the north and west, and the Bobolink, which was quite common in the dike lands about Canning and the Basin of Minas, was only occasional in this southern Barrington district.

The past summer, 1908, I spent at Chester, Nova Scotia, a small village at the head of Mahone Bay, an inlet of the Atlantic, fifty miles south of Halifax and about one hundred and fifty miles north along the coast from Barrington. The region was in every way similar to that about Barrington, but here at Chester I found the Chipping Sparrow and the Goldfinch relatively abundant, yet at no time was either of these birds ever seen at Barrington, though habitat conditions there were equally favorable for both. How far southward these species extend beyond Chester I am unable to say, but the fact remains that they do not appear in the fauna of the lower part of the peninsula, at least so far as my six summers of observation and collecting about the Barrington region are concerned.

The solution of this rather curious local distribution of two such widely spread species as the Chipping Sparrow and the Goldfinch appears to me to be involved in a geological change, and to date back to a time when Nova Scotia was severed from the mainland, where what is now a low-lying and partly marshy tract of country which forms the present neck or isthmus that separates the waters of Northumberland Strait on the north from those of Chignecto Bay, at the head of the Bay of Fundy, on the south. This region, which we may call the Amherst district, from the principal town situated there, is evidently an uplift of comparatively recent geological date. Nova Scotia was unquestionably at one time an island, severed from the rest of the continent by a strait, probably of some width, which connected the two bodies of water mentioned above. How wide a stretch of water this strait may have embraced it is difficult to say. Prince Edward Island is now separated from the

mainland by Northumberland Strait of a varying width of from nine to thirty miles. There is evidence of considerable submergence in the region about Amherst as Sir J. W. Dawson has shown in his 'Acadian Geology' (4th ed., 1891, pp. 29–31). Submerged forests, mainly of pine and beech, have been found in several localities about Cumberland Basin and Cobequid Bay, and the great 'dikes' about the Basin of Minas, which are reclaimed maritime marshes, Dawson regards as undergoing slow submergence. All these facts indicate at least, an unstable condition, and taken together with the low relief of the region as a whole and the present general relations of land and water we are justified, I think, in believing that this strait once existed, and that at a not very remote period. Furthermore, there is much evidence to show that considerable areas along the northeastern coast of the continent have suffered submergence under the enormous weight of the ice mass that was pushed seaward from the Laurentide Glacier.

The relative distribution of land and water areas unquestionably exerts an important influence in determining the range of various species of land birds. Many land birds migrate over wide stretches of sea, but, as Wallace has pointed out, such routes possibly indicate a former land surface that has become gradually submerged. The observations of Mr. Wells W. Cooke would seem to disprove this, as the evidence he has gathered regarding the Gulf and Caribbean routes indicate that migrating birds frequently follow courses that lead over the deeper parts of these waters. In the problem before us, however, we are dealing with more than the purely migratory impulse. This migratory impulse *per se*, I take it, is the primitive instinct of certain species of birds to reach a northerly region where food of a suitable kind for the young is abundant and where the summer day is long, giving the maximum light conditions under which to forage.[1] After a bird has reached this summer home it will constantly tend to widen its breeding area, spreading out over a larger territory, limited of course by various ecological factors, as suitable habitat conditions, by the pressure of other species, by the nature and abundance of food, by temperature, and by the conformation of land and water areas. The entire

[1] See article by E. A. Schäfer, F. R. S., 'On the Incidence of Daylight as a Determining Factor in Bird Migration.' Nature, Dec. 19, 1907.

phenomenon of migration may possibly have originated as an extension of a once more southerly breeding range of various species of birds which followed the widening zone of green and the development of insect life northward in the wake of the receding ice sheets. The individuals of a species that spread farthest to the north became the migrating element, passing over the intervening areas.

The present land bird fauna of Nova Scotia may have been derived from two faunal stocks — a more primitive boreal one that has occupied the region from remote times, and a later transition fauna which has invaded the peninsula since the reëlevation of the previously sunken isthmus. This somewhat venturesome statement appears to be borne out by certain facts. Many of the boreal types belong to genera of widespread distribution in both the Nearctic and Palæarctic regions. Such for example are *Pinicola*, *Carpodacus*, *Loxia*, *Spinus*, *Sitta*, *Regulus*, *Certhia*, and *Parus*. These may have occupied the region even during glacial conditions, for glaciers do not preclude a forest growth and food would be abundant during the short breeding season. Furthermore, these forms probably spread around the subarctic zone in Pleistocene times when possibly, as many geologists believe, a more extensive land relation existed between the eastern and western continental land masses than at present. Indeed, these genera may have a still older history, dating back to the Middle Tertiary, with a more decidedly polar distribution, but this is purely speculative and we have no evidence, fossil or otherwise, in support of this view. These boreal types, as we know, are wide rangers and the glacial winters would find them foraging to the southward, along the borders of the crowded Austral life zone. Narrow straits would offer no barrier; more than likely there was a much greater land area and wider land connections than at present when these hardy species made their seasonal shifts through the then subarctic forests of the region now embraced by Lower Canada and the northeastern United States. The present irregular movements of these birds may possibly be the result of a habit of wandering widely in search of food, impressed upon them by the precarious conditions of existence during the Glacial Period.

The purely American element in the present boreal fauna, such as the Thrushes, the several species of Wood Warblers, the Junco,

White-throated Sparrow, the Flycatchers and others mentioned above, seem to me to form a group that established themselves as breeders in the boreal zone at an early day after the uncovering of the land by the retreating glaciers, spreading into the Nova Scotia peninsula most likely soon after or possibly during the rcëlevation of the land bridge. In reality they do not belong to the ancient boreal fauna as just outlined, but represent an early advance movement of the more southern bird life, a movement that is still in progress. These birds are all typical long distance migrants rather than wanderers and, unlike the true boreal wanderers, they leave a wide hiatus of unoccupied territory between their breeding grounds and their winter quarters. This is especially true of the Thrushes, Wood Warblers, the Vireo, and Flycatchers which feed on fruits, winged insects, and soft larva, while the seed-eating species like the Junco, the White-throated and other Sparrows, are not compelled to move so far and hence occupy a winter zone of territory much nearer to their breeding haunts. Yet even such northerly breeders as the Fox Sparrow and the White-crowned Sparrow leave a considerable breadth of unoccupied territory between their summer and winter ranges.

Sometime during the post-glacial period many purely transition or Alleghanian species spread into the Nova Scotia region, probably by way of the land connection, but the significant fact is that this movement is still going on and that some species, like the Chipping Sparrow and possibly the Goldfinch, have not yet invaded the entire territory. That they have come by the Amherst neck of land from the main continent is also evident since these birds do not appear to have reached as yet the more southern districts of the peninsula, at least along the eastern side, so far as my observations go. Still more significant is the support given to this view by Downs in his 'Catalogue of the Birds of Nova Scotia' [1] in remarking upon certain species. From what I gather his observations are chiefly in the neighborhood of Halifax and in the more western parts of the Province. Of the Chipping Sparrow he says: "Lately became rather common"; of the Field Sparrow, "not very com-

[1] 'A Catalogue of the Birds of Nova Scotia,' by A. Downs. Proceedings and Transactions of the Nova Scotia Institute of Natural Science, Vol. VII, pp. 142–178, 1888.

mon"; of the Rose-breasted Grosbeak, "not common about Halifax, but of more frequent occurrence in the vicinity of Truro and Pictou" (Truro and Pictou are toward the west and nearer the Amherst district). The Goldfinch Downs speaks of as common. Of the Red-winged Blackbird he says: "very rare .... A few occur in the western part of the Province," and of the Meadowlark, "Very rare. Only a mere straggler." These are significant statements regarding two such widespread birds, especially the reference to the Red-wing occurring in the western part. The Vesper Sparrow he speaks of as a "common summer resident" though I never saw it about Barrington and Chester, nor did I see either the Field Sparrow or the Rose-breasted Grosbeak. Of the Catbird, which I found sparingly the first summer (1901) about the villages at Barrington, Downs says: "Rather common..... It does not arrive until the summer is well advanced. Breeds in alder swamps." This lateness of arrival, together with its apparently irregular appearance, may indicate a tardiness in the general northeastern extension of this species' range. The House Wren and the Thrasher are not included in Downs's list, nor have I ever observed these birds in the Province. The Ruby-crowned Kinglet is spoken of as uncommon, and this enlightening observation is made in regard to the Bluebird: "Uncommon. I have seen it breeding in an apple tree at Kentville. It appears to be getting a footing in Nova Scotia." I may add that I have never met with the Bluebird in the Province though I found it much farther north — on the north shore of the St. Lawrence near Les Eboullements in the Province of Quebec, and Dr. Dwight has recently reported it from Tadousac in the same region.[1]

Further confirmatory evidence in regard to the extension of the range of certain birds is given by Dr. Dwight in his 'Summer Birds of Prince Edward Island'[2] where he speaks of the Chipping Sparrow as "Not a common species, and only occasionally observed." Of the Goldfinch he notes, "a few seen almost daily." Of the Vesper Sparrow Dr. Dwight says: "An abundant bird, frequenting the open fields in the more settled districts." Neither the Catbird nor the Bluebird are recorded by Dr. Dwight in this

[1] Auk, Vol. XXVI, Jan., 1909, p. 83.
[2] *Ibid.*, Vol. X, Jan., 1893, p. 1.

Prince Edward Island list, and it is quite possible that these birds have not yet found their way across Northumberland Strait, while they certainly have invaded the Nova Scotia peninsula, though sparingly, by way of the isthmus. The Red-winged Blackbird and the Meadowlark likewise are not included in Dr. Dwight's list, though recorded by Downs in Nova Scotia as above mentioned.

These facts, it seems to me, point pretty conclusively to the gradual extension of certain species of birds into an area formerly separated from the main mass of the continent. Nova Scotia offers a singular proof of the use of a land route, for it would seem that birds had found their way into the region by the Amherst isthmus, as evinced by the occurrence of a number of species in localities comparatively near to this district, while still absent, or only occasional, in the more southern and eastern parts of the Province. Most of these species, also, as recorded by Downs, are still comparatively uncommon. In a list of birds observed at Pictou, N. S., from January to July, 1895, by W. A. Hickman,[1] the Chipping Sparrow, Field Sparrow, and Goldfinch are mentioned as very common breeders, but the Catbird, the Bluebird, and the Red-winged Blackbird and Meadowlark are not included in these observations.

Taking a broad view of the problem it would seem that there is some evidence for entertaining the idea that the extension of species into more northerly breeding grounds is a phase of distribution that is still going on; that our so-called "faunas" — Carolinian, Alleghanian, and Canadian — in reality represent a somewhat temporary state of groups of species in relation to breeding areas, and the more or less arbitrary boundaries of these faunas represent our knowledge only of the present conditions of distribution in a gradual and general northward movement of considerable antiquity. Mr. Witmer Stone has furnished me with some interesting facts relating to the northward extension of certain Carolinian birds into the Alleghanian, and even into the Canadian, zones of Pennsylvania.[2] About Harvey's Lake, Luzerne Co., and at Lopez, Sullivan Co., since the cutting off of the hemlock timber over considerable areas, the Yellow-breasted

[1] See Ottawa Naturalist, Vol. IX, p. 230.

[2] Stone, 'Birds of Eastern Pennsylvania and New Jersey.'

Chat, a bird regarded as characteristic of the Carolinian fauna, has made its appearance as a breeder, while the Chewink, a species of decidedly austral range, rarely going beyond the transition zone, has likewise invaded these localities. Mr. Richard C. Harlow,[1] records the Tufted Titmouse and the Yellow-breasted Chat in the decidedly Canadian element of Pike Co., Pennsylvania. Undoubtedly the conditions incident to 'second growth' are largely a determining factor in this invasion of new territory, for the opening up of a tract of country to more sunlight would certainly bring about an environment not unlike the typical Carolinian region further south. Still the individuals of these species must have the tendency to move northward farther than their apparent faunal limit, otherwise they would not find these favorable spots in new territory. Most likely they invade the region by way of the river valleys, spreading out into the surrounding districts.

Dr. Merriam has accumulated a vast amount of evidence to show the control exerted by temperature in the distribution of living organisms.[2] But is not this temperature relation more apparent than real, a temporary adjustment to the environing conditions which the temperature brings about rather than a hard and fast relation between temperature and the organism direct? The whole question is recondite, but it seems hardly possible for such closely related species as, for example, the Wood Thrush, the Veery, and the Gray-cheeked Thrush to be so profoundly influenced by temperature alone as to have their northward breeding ranges so widely different. Rather it seems to me each form represents either a pioneer or a laggard movement, as the case may be, in a general tendency of various species of birds to spread gradually northward into a region of new environing conditions which has been opened to them since the Glacial Period. The Canadian fauna, barring the more or less circumpolar forms, thus represents an advance group of species that spread into northerly breeding grounds at a probably early day after the disappearance of glacial conditions; the Alleghanian fauna that of species that spread at a later date and are still spreading into new

[1] 'Summer Birds of Western Pike county, Pennsylvania.' Cassinia, 1906, pp. 16–25.

[2] 'Laws of Temperature Control of the Geographical Distribution of Terrestrial Animals and Plants.' National Geographic Magazine, Vol. VI, 1894. pp. 229–238.

territory, while the Carolinian birds are the laggards in this northward movement. Each group or fauna has become more or less adapted to certain characteristic conditions within the area in which they have established themselves as breeders. Some of the Carolinian species, as the Cardinal, the Carolina Wren, the Tufted Titmouse, and the Turkey Buzzard show but a slight tendency to recede from their breeding range during the winter, owing, no doubt, to the less northerly position which they have attained. Toward the northwest where a wide expanse of territory has been open since the Glacial Period many species of birds which breed widely throughout the Transition zone have spread as far north as the Great Slave Lake, reaching even to the edge of the Barren Grounds.[1]

The problem as to the primitive centers of distribution from which our bird fauna was originally derived has been so ably set forth by Dr. J. A. Allen in his article on 'The Geographical Origin and Distribution of North American Birds, considered in Relation to Faunal Areas of North America',[2] that there is little left to say upon the subject. Students of ornithology and of geographical distribution in general owe Dr. Allen a lasting debt of gratitude for his comprehensive presentation of the facts and his illuminating deductions therefrom. It would appear from Dr. Allen's review that sometime during the Tertiary Period, possibly as early as the late Miocene, there was a spreading out toward the east of certain types of birds which find their center of development to-day in the Plateau Region of southwestern North America and Mexico. Such forms as the Chewink, the Thrasher, and the Bluebird are certainly of plateau origin and the same is probably true of the Bob-white and the Wild Turkey. A second and large element in our eastern bird fauna is of tropical origin, derived from Middle and South America. To quote Dr. Allen[3]: "Our Vultures, several genera of our Hawks and Owls, our Cuckoos, most of our Woodpeckers, our Nighthawks, Whippoorwills, Swifts, and all of our Hummingbirds; all of our Flycatchers, Orioles, and Blackbirds,

[1] See Preble, North American Fauna, No. 27. 'A Biological Investigation of the Athabasca-Mackenzie Region.' 1908.

[2] The Auk, Vol. X, p. 97. April, 1893.

[3] Dr. Allen, in his paper, is speaking for the entire country, not the eastern part alone, to which the present article is confined.

and our Vireos and Tanagers; many of our Sparrows and Grosbeaks; all of our Gnatcatchers, and the Mockingbirds, some of our Wrens, and a few of our more southern genera of Warblers, as the Yellowthroats and Redstarts," are clearly of tropical origin. Probably this influx of plateau and tropical types into the eastern region was a very slow and gradual movement which took place during and after the addition of the marginal Tertiary seafloor to the southeastern portion of the continent, which increased the land area to the extent of the present southern and Atlantic coastal plain. Much of Cuba, the peninsula of Yucatan, and the eastern seaboard of Mexico was uplifted about this time. A third element appears to have had its origin within the limits of the region itself, though many of the genera are represented by numerous species in the western portion of the continent. Of the more strictly eastern genera may be mentioned *Dolichonyx*, *Mniotilta*, *Protonotaria*, *Helinaia*, *Helmitherus*, *Helminthophila* (the larger number of species), *Dendroica* (mainly eastern), *Siurus*, *Oporornis*, *Sylvania*, *Galeoscoptes*, *Cistothorus*, and *Telmatodytes*. The fourth element in our bird fauna is the Old World boreal group of genera already mentioned and a number of species of pronounced Old World affinities, as the Robin, the Hylocichline Thrushes, the Titlark, the Barn, Cliff, and Bank Swallows, the Shrikes, Crows, and Shore Larks, which have been more or less modified from Palæarctic types.

It is next to impossible to say in which portion of the continent many of the purely indigenous or autochthonous forms had their origin, for they are spread across the land from ocean to ocean in a succession of closely allied species or as local races. This is especially true of most of our genera of indigenous sparrows. Undoubtedly there occurred sometime during middle and late Tertiary times an extension of plateau types into the humid Eastern Province, and, conversely, a spread of eastern forms into the arid districts of the Plateau region, while at the same time an influx of tropical forms made their appearance, coming probably in the main from a tropical land area in the southwest and following the widening Gulf margin of the continent. How far north this preglacial bird fauna of diverse origin may have spread it is impossible to say, but some forms, even of tropical origin, undoubtedly

reached a high latitude, very probably during the warm Miocene and early Pliocene times, and their descendants may possibly now be represented by those migrants which breed far within the limits of the Boreal Zone. During Miocene times there were extensive land connections between Asia and Northwest America and very likely a much closer land relation between Europe and America. It was during this time, no doubt, that the influx of our Palæarctic types occurred, and it is a significant fact that all of these genera are of extensive range and of markedly northern distribution, such for example as the Passerine genera *Merula, Regulus, Parus, Sitta, Certhia, Anthus, Hirundo, Petrochelidon, Riparia, Ampelis, Lanius, Pinicola, Carpodacus, Loxia, Acanthis, Passerina, Calcarius, Corvus,* and *Otocoris.*

Throughout an immense lapse of time, time that must be reckoned in hundreds of thousands of years, during which the great Keewatin and Laurentide glaciers pushed their ice sheets beyond the present site of the Great Lakes and the Mohawk Valley, forcing southward the animal and plant life into an area of high biotic tension, a widespread change in types must have taken place. The more primitive forms have undoubtedly disappeared. Only occasionally may we pick up a trace of this ancestry in some fleeting juvenal phase of plumage. Modifications of type went on; differentiation into new genera, species, and varieties through molecular changes in pigmentation, in size and shape of bill and feet, of wings and tail, and in the deep-seated structure of the germ plasm. Diversity of structure went hand in hand with diversity of habit and of habitat. It was a period of profound environmental moulding, intensified by the effect of the glaciers on the land and its life. From our limited point of view the array of species and varieties which we see to-day seem peculiarly stable in their features and their adaptations. But the dynamic influences of environment are ceaseless if inconspicuous. Species and faunas alike are but passing phases in the vast cosmic processes of a continent's history.